

Long-term Dreissenid Impacts on Water Clarity in Lake Erie

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ABSTRACT. Since shortly after their introduction, dreissenid mussels have been thought to have improved water clarity in Lake Erie, particularly in the western basin. However, long-term monitoring (1982–2004) has found no evidence of persistent, basin-wide increases in water clarity in either the western or the central basin of Lake Erie since the *Dreissena* invasion. In fact, spring water clarity in both of those basins has exhibited statistically significant declines in the post-dreissenid period. In contrast, chlorophyll *a* levels in the western basin have declined by about 50% since the *Dreissena* invasion during both spring and summer. The discrepancy in the responses of water clarity and chlorophyll *a* is probably a consequence of both the large sediment loads entering the western basin and resuspension of unassimilated non-algal particulates. In the eastern basin, spring transparency has increased substantially and turbidity has decreased since *Dreissena* colonization, in spite of the much greater depth of this basin. This is probably due to higher mussel densities and the lack of major sources of turbidity in that basin. Summer turbidity has also decreased markedly in the eastern basin, although thermal stratification during this period would probably preclude direct filtration effects. Instead, we hypothesize that reductions in whiting events due to calcium uptake by dreissenids have contributed to the summer decreases in turbidity seen in the eastern basin.

INDEX WORDS: *Dreissena*, Secchi depth, turbidity, chlorophyll.

INTRODUCTION

Shortly after their discovery in the Laurentian Great Lakes system in 1988 (Hebert *et al.* 1989), zebra mussels (*Dreissena polymorpha*) became established throughout the western basin and most of the central basin of Lake Erie, and had completely colonized all three basins by the end of 1989 (Griffiths *et al.* 1991). In the first years following the invasion, estimates of population densities in the western basin exceeding 340,000 individuals/m² were reported (MacIsaac *et al.* 1991, Leach 1993), as were correspondingly high filtering rates of up to 132 m³/m² (MacIsaac *et al.* 1992). This, coupled with reports of localized increases in transparency in the western basin of Lake Erie (Leach 1993, Holland 1993) and dramatic declines in phytoplankton biovolume at nearshore sites in the lake (Nicholls and

Hopkins 1993), has led to a wide-spread perception amongst both the lay public and the scientific community that dreissenids have “cleaned up” the western basin of Lake Erie.

Subsequently, a second, deeper-living congener, *D. bugensis*, was discovered in the offshore sediments of the lake (Dermott and Munawar 1993). In recent years it appears that dreissenid populations in the lake have shifted from *D. polymorpha* to *D. bugensis*, with the result that biomass has been increasing in deeper regions of the lake (Dermott *et al.* 1998, Jarvis *et al.* 2000). This raises the possibility that dreissenid impacts might become relatively more pronounced in deeper areas of the lake.

Lake Erie is divided morphometrically into three distinct basins, which differ in terms of both topography and trophic condition (Burns 1985), and can therefore be expected to exhibit differing responses to perturbations. The western basin is shallow, with a mean depth of 7.4 m, and does not exhibit stable

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stratification during the summer (Mortimer 1987). The high surface area/volume ratio and lack of a thermal barrier might make this region the most susceptible to dreissenid effects. On the other hand, this basin also receives the largest inputs of nutrients and suspended sediments, and is generally the most turbid region of the lake (Mortimer 1987), factors which might mask potential dreissenid impacts. The offshore of the central basin has a fairly uniform bottom of 20–24 m and typically stratifies in the summer (Green 1960). It is subject to inputs of sediments from the western basin (Mortimer 1987) as well as from bluff erosion (Kemp *et al.* 1977), and given its shallowness is also susceptible to sediment resuspension (Charlton and Lean 1987). The eastern basin, with a mean depth of 24 m and a maximum depth of 64 m, stratifies stably during the summer (Green 1960) and has the lowest inputs of both nutrients and sediments (Mortimer 1987, Kemp *et al.* 1977).

In this study we assessed whether persistent changes in water clarity have occurred in any of the three basins of Lake Erie since the invasion of dreissenid mussels. We were particularly interested in determining if long-term, basin-wide increases in transparency have occurred in shallow areas of Lake Erie, as is commonly assumed, and whether dreissenid mussels have had an impact on the deeper, offshore waters of the eastern basin of the lake. An earlier report from our program (Makarewicz *et al.* 1999) presented data from the first 4 to 5 years of the dreissenid invasion and did not find significant increases in water clarity in the western basin, although reductions in spring (but not summer) chlorophyll *a* were noted in that basin. Here we expand upon that earlier study with a dataset that extends 16 years past the initial *Dreissena* invasion.

METHODS

The data used in this study were generated from the annual monitoring of the Laurentian Great Lakes conducted by the U.S. Environmental Protection Agency's Great Lakes National Program Office (GLNPO) between 1983 and 2004. Sampling is spatially extensive throughout the offshore waters (Fig. 1), with surveys conducted during the spring isothermal period (generally April) and the summer stratified period (August). Prior to 1994, multiple runs on each lake were typically undertaken during each cruise. In order to ensure data comparability through time, only those cruises with dates most

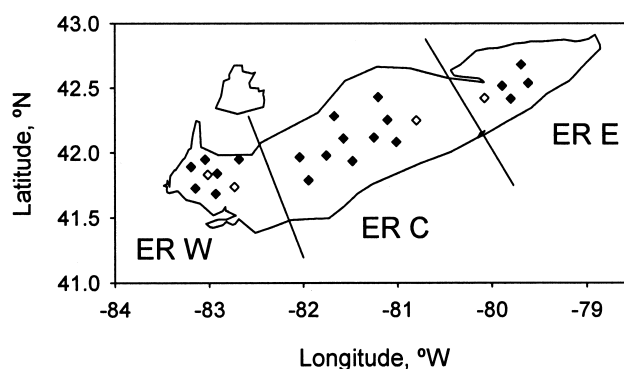


FIG. 1. Map of Lake Erie indicating location of the sampling stations. Stations denoted with hollow symbols were not sampled in all years. Division of lake into three basins (western: ER W; central: ER C; and eastern: ER E) is shown.

closely approximating the average date for each seasonal cruise were included in our analyses, except in the case of Secchi depths, for which the relative infrequency of measurements occasionally necessitated using data from the next closest cruise date.

At each station, both discrete and composite samples were taken with Niskin bottles mounted on a SeaBird Carousel Water Sampler. Spring analyses utilized both discrete and composite (composed of samples from 1 m, 5 m, 10 m, and 20 m) samples collected from depths ≤ 20 m, while summer analyses utilized "surface" (i.e., 1 m) samples. Prior to 1999, chlorophyll *a*, corrected for pheophytin, was determined on a Turner Designs 10-AU fluorometer after extraction in 90% acetone. After 1999, chlorophyll was measured using narrow band optical filters, following the method of Welschmeyer (1994). Turbidity was determined onboard ship just subsequent to sampling using a nephelometer, and reported in NTU.

Pre-dreissenid years were defined as being 1983–1988 in the western and central basins, and 1983–1989 in the eastern basin. Differences between pre- and post-dreissenid years were assessed separately for each basin, using a generalized linear model, with dreissenid period a two-level (pre and post) fixed effect, station a random effect, and year a fixed effect nested within dreissenid period. Significance was assessed at $\alpha = 0.05$. Data were log-transformed prior to analysis to conform to the assumptions of normality and homoscedasticity.

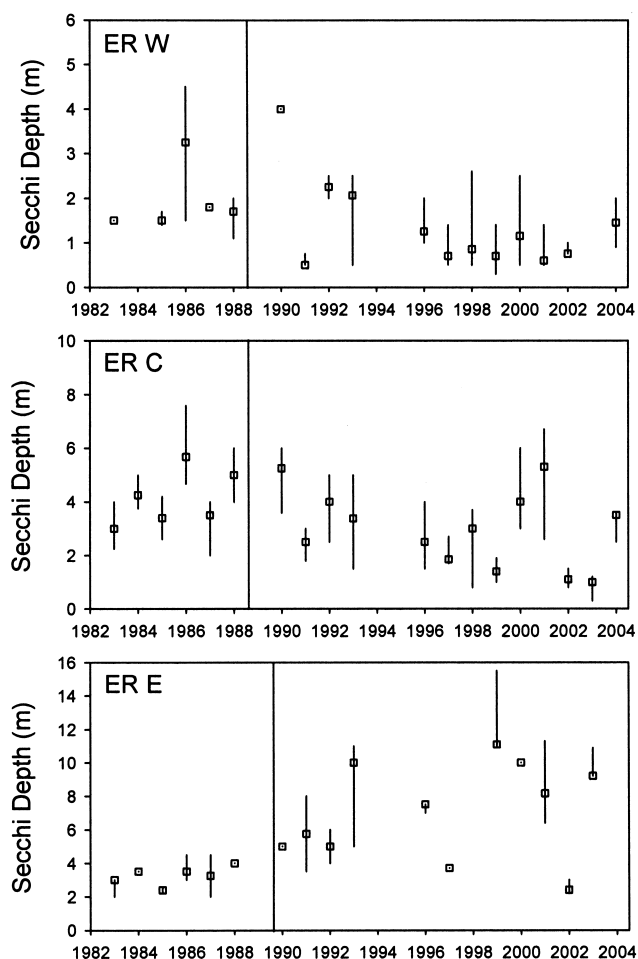


FIG. 2. Secchi depths for the western (ER W), central (ER C) and eastern (ER E) basins during spring cruises. Symbols indicate medians, vertical lines indicate ranges. Vertical control lines separate pre- from post-dreissenid periods.

RESULTS

Spring

During the spring, the western and central basins exhibited similar changes in water clarity (as measured by Secchi depth) and turbidity after the *Dreissena* invasion. Rather than increasing, Secchi depth showed statistically significant decreases in both basins after the *Dreissena* invasion (Fig. 2, Table 1). Correspondingly, the average turbidity during the post-*Dreissena* period in both basins was approximately double the pre-*Dreissena* average (Fig. 3), differences which were statistically significant (Table 1). In spite of the decrease in transparency and the generally higher turbidity values, though, spring chlorophyll *a* values in the western basin of

Lake Erie showed a distinct and sustained decrease after the invasion of *Dreissena*, with post-*Dreissena* values averaging less than half of pre-*Dreissena* values (Fig. 4). No trend in chlorophyll *a* was seen in the central basin.

The situation was quite different in the eastern basin, where Secchi depths more than doubled, on average, after the *Dreissena* invasion (Fig. 2, Table 1). The change in Secchi depth was not immediate, but increased gradually to reach maximum values in the late 1990s. Individual Secchi depths during the pre-*Dreissena* period ranged from 2.0 to 4.5 m ($\bar{x} = 3.2$ m), while values between 1990 and 1997 varied between 3.7 and 11 m ($\bar{x} = 6.7$ m). With the exception of 2002, a year of unusually low water clarity, average annual Secchi depths since 1999 have remained above 8.0 m. Turbidity showed a similar trend (Fig. 3, Table 1), with values between 1990 and 1997 approximately half those of the pre-*Dreissena* period ($\bar{x} = 1.0$ and 1.9 NTU, respectively), and a further decrease in turbidity seen since 1999 ($\bar{x} = 0.65$ NTU). Chlorophyll *a* values were lower on average after 1992, with the exception of an unusually high value in 2001; however, there was no statistically significant difference between the pre- and post-*Dreissena* periods (Table 1).

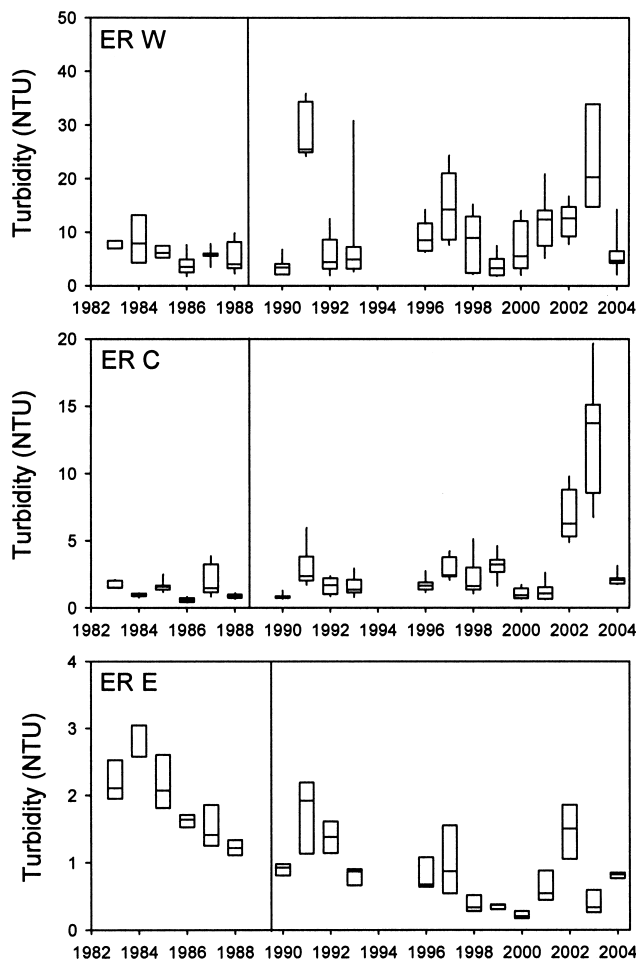
Summer

The *Dreissena* invasion had no apparent impact on either water clarity (Fig. 5) or turbidity (Fig. 6) in the western basin during summer; neither variable showed a statistically significant change after the arrival of dreissenids (Table 2). In contrast, chlorophyll *a* concentrations decreased substantially, with the mean post-*Dreissena* concentration just more than half of the pre-invasion value (Fig. 7, Table 2). There are substantial gaps in our data, notably 1990 and 1992 - 1995, which make it difficult to assess the time course of this change, particularly in the early years of the invasion. The two earliest post-invasion years for which we have data (1989, 1991) did not appear to differ from pre-invasion years, but by 1996 chlorophyll *a* had decreased substantially, and though concentrations have shown a slight upwards trend in the most recent years of our dataset, they remain at levels substantially below those seen during the pre-*Dreissena* period.

A modest but statistically significant increase in average summer Secchi depth was seen in the central basin after the *Dreissena* invasion (Fig. 5, Table 2). This increase, on the order of approximately 8%, appeared to be due to unusually low Secchi depths in

TABLE 1. Generalized linear model results for spring Secchi depth, turbidity and chlorophyll *a*. ER W = western basin; ER C = central basin; ER E = eastern basin. Df1 and MS1 refer to main factor effects (i.e., pre and post-dreissenid periods); df2 and MS2 refer to interaction effects (i.e., station \times period). Significant *P* values for main factor effects ($\alpha = 0.05$) are shown in bold; increases are identified by (+), decreases by (-). Mean values for pre- and post-dreissenid periods are also shown.

Basin	df1	df2	MS1	MS2	F	P	\bar{x} pre	\bar{x} post
Secchi Depth								
ER W	1	5	0.303	0.031	9.7	0.027-	2.21	1.31
ER C	1	9	0.724	0.017	42.0	> 0.001-	4.39	2.84
ER E	1	3	0.332	0.003	96.2	0.002+	3.24	7.80
Turbidity								
ER W	1	5	0.185	0.009	21.3	0.006+	5.80	10.94
ER C	1	9	2.263	0.027	84.3	> 0.001+	1.26	3.22
ER E	1	3	2.130	0.002	1,128.3	> 0.001-	1.88	0.84
Chlorophyll								
ER W	1	5	1.178	0.079	14.9	0.012-	7.58	3.10
ER C	1	9	0.065	0.034	1.9	0.198	3.44	4.24
ER E	1	3	0.003	0.049	0.1	0.821	1.33	1.61



the 2 years just prior to, and unusually high Secchi depths in the 2 years subsequent to *Dreissena* establishment. Disregarding these 4 years, the opposite trend was apparent: Secchi depth declined from a pre-*Dreissena* average of 7.7 m to a post-*Dreissena* average of 6.5 m (F ratio = 22.7; $p = 0.001$). Turbidity showed a statistically significant decrease after the *Dreissena* invasion, although this difference was slight (Fig. 6, Table 2). Chlorophyll *a* was also significantly lower during the post-*Dreissena* period (Fig. 7, Table 2), although this change, amounting to a decrease of 36%, was not as pronounced as that seen in the western basin. As in the western basin, chlorophyll *a* concentrations did not appear to change during the first few post-invasion years for which we have data, and reached a minimum during the late 1990s. Concentrations have shown a tendency to increase in the most recent years for which we have data, as was the case in the western basin,

FIG. 3. Box plots of turbidity values (measured as NTU) for the western (ER W), central (ER C) and eastern (ER E) basins during spring cruises. Boxes indicate 25th and 75th percentiles; horizontal lines indicate median; vertical lines indicate 10th and 90th percentiles. Vertical control lines separate pre- from post-dreissenid periods.

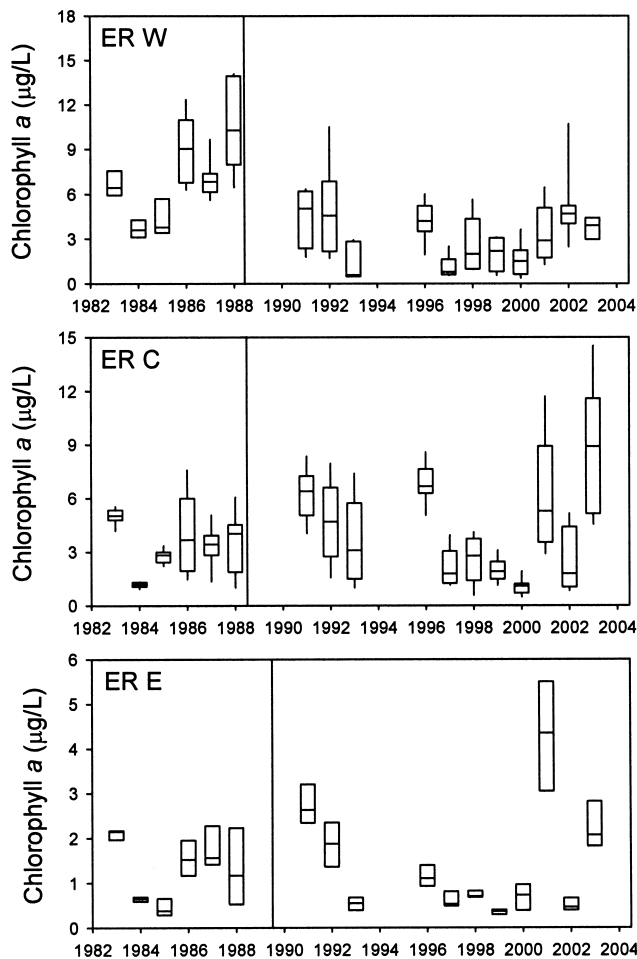


FIG. 4. Box plots of chlorophyll *a* ($\mu\text{g/L}$) values for the western (ER W), central (ER C) and eastern (ER E) basins during spring cruises. Boxes as in Figure 3. Vertical control lines separate pre- from post-dreissenid periods.

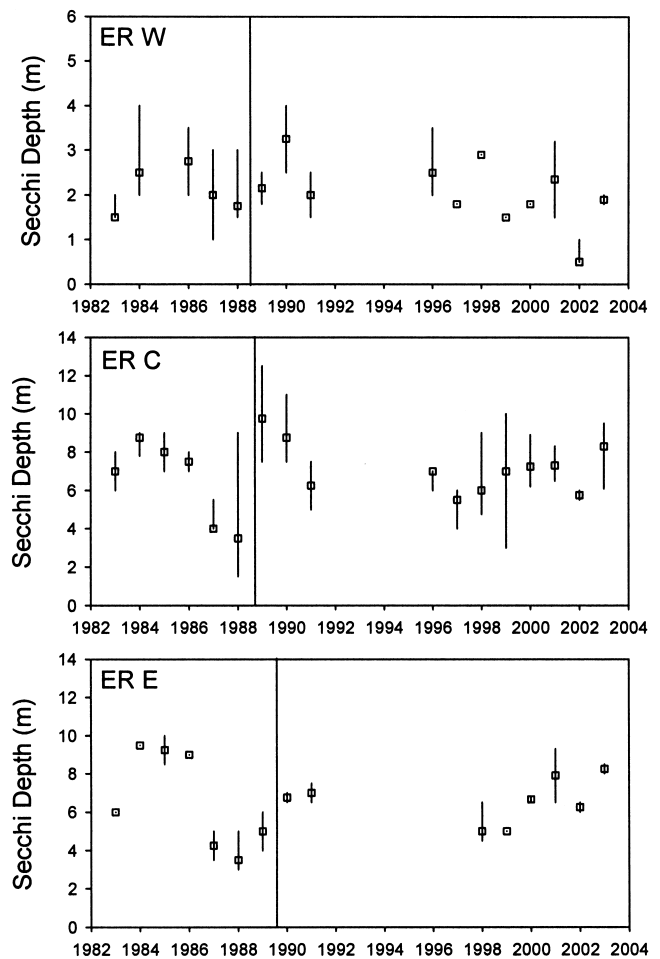


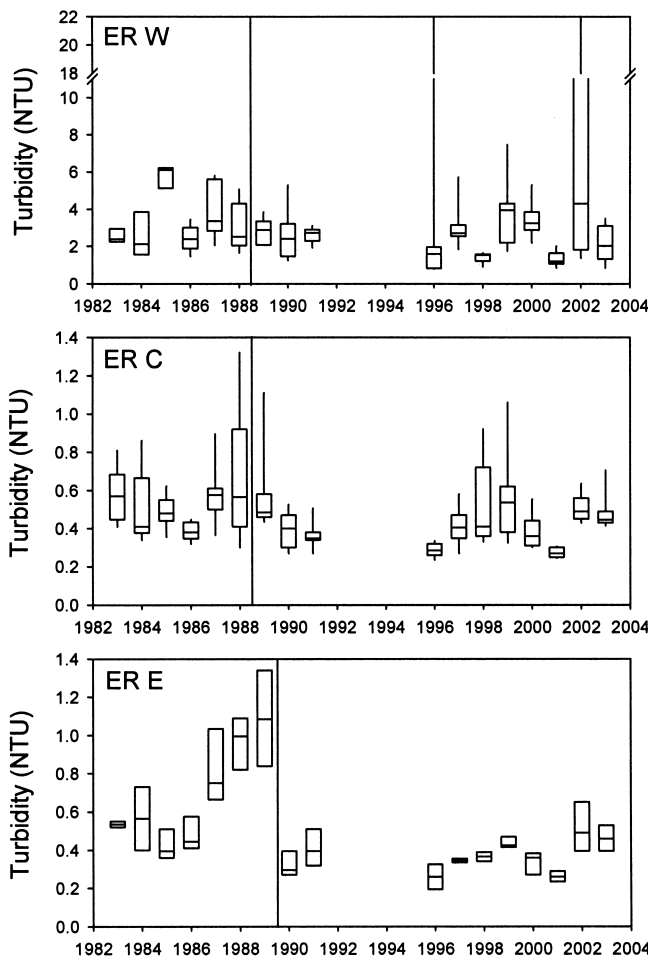
FIG. 5. Secchi depths for the western (ER W), central (ER C) and eastern (ER E) basins during summer cruises. Symbols indicate medians, vertical lines indicate ranges.

but have still tended to be lower than those in the pre-*Dreissena* period.

No change in summer Secchi depth was seen in the eastern basin after the *Dreissena* invasion (Fig. 5, Table 2), although post-invasion turbidity did show a statistically significant decline (Fig. 6, Table 2). This difference was more substantial than that seen in the central basin, constituting a decrease in average turbidity of over 60% after the invasion, although the general pattern of post-*Dreissena* turbidity in the two basins was remarkably similar. As in the central basin, a modest decrease in average chlorophyll *a*, amounting to 25%, was seen after the invasion (Fig. 7, Table 2).

DISCUSSION

The perception that Lake Erie, and the shallow western basin in particular, has experienced an increase in transparency since the *Dreissena* invasion seems to be based primarily on two early reports which examined localized effects during the first few post-invasion years (Leach 1993, Holland 1993). In contrast, an earlier report from our program failed to find any increases in transparency in the western basin during the 5 years following *Dreissena* establishment (Makarewicz *et al.* 1999). Using a longer term dataset, our study has also found no evidence of persistent, basin-wide increases in transparency in either the western or the central basins of Lake Erie;



in fact, spring transparency has been somewhat lower in both of those basins since *Dreissena* colonization. While there was some suggestion of an increase in summer transparency in the central basin in the two years immediately following the invasion, this has not persisted. In contrast to the western and central basins, transparency did increase substantially during the spring in the much deeper eastern basin, however. Previous studies have noted an increase in Secchi depths in the eastern basin in the years immediately following the *Dreissena* invasion (Howell *et al.* 1996, Makarewicz *et al.* 1999), and our results indicate that this increase has continued to the present.

While transparency and turbidity in the western basin did not show the expected responses to the dreissenid invasion, both spring and summer chlorophyll *a* concentrations did show substantial decreases after the invasion. This suggests that mussel populations in this basin were capable of impacting particle concentrations, and that these impacts were sufficient to overcome phytoplankton growth rates,

FIG. 6. Box plots of turbidity values (measured as NTU) for the western (ER W), central (ER C) and eastern (ER E) basins during summer cruises. Boxes as in Figure 3. Vertical control lines separate pre- from post-dreissenid periods.

TABLE 2. Generalized linear model results for summer Secchi depth, turbidity and chlorophyll
a. ER W = western basin; ER C = central basin; ER E = eastern basin. Df1 and MS1 refer to main factor effects (i.e., pre and post-dreissenid periods); df2 and MS2 refer to interaction effects (i.e., station \times period). Significant *P* values for main factor effects ($\alpha = 0.05$) are shown in bold; increases are identified by (+), decreases by (–). Mean values for pre and post-dreissenid periods are also shown.

Basin	df1	df2	MS1	MS2	F	P	\bar{x} pre	\bar{x} post
Secchi Depth								
ER W	1	5	0.012	0.008	1.5	0.274	2.21	2.20
ER C	1	9	0.071	0.011	6.5	0.031+	6.57	7.12
ER E	1	3	0.001	0.003	0.41	0.565	6.11	6.59
Turbidity								
ER W	1	5	0.038	0.037	1.0	0.357	3.27	4.67
ER C	1	9	0.355	0.020	17.7	0.002–	0.55	0.44
ER E	1	3	0.936	0.033	28.8	0.013–	0.73	0.37
Chlorophyll								
ER W	1	5	0.464	0.023	19.9	0.007–	11.40	6.06
ER C	1	9	1.323	0.032	41.0	> 0.001–	3.01	1.92
ER E	1	3	0.416	0.006	72.2	0.003–	2.16	1.63

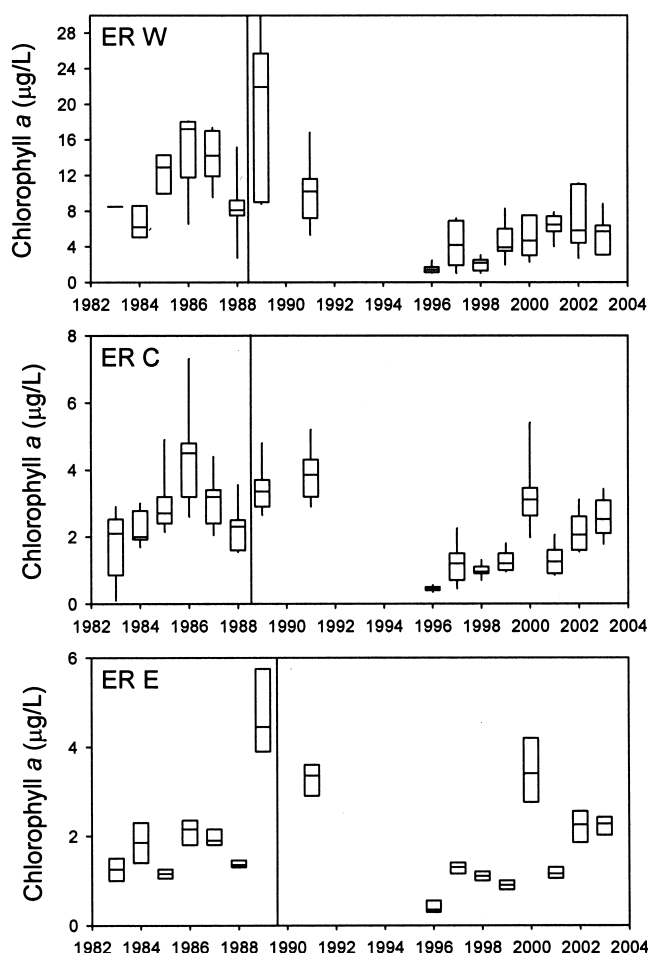


FIG. 7. Box plots of chlorophyll *a* ($\mu\text{g/L}$) values for the western (ER W), central (ER C) and eastern (ER E) basins during summer cruises. Boxes as in Figure 3. Vertical control lines separate pre- from post-dreissenid periods.

but not inputs of non-algal particulates. Algae make up a relatively small percentage of suspended solids in the western basin—typically 5% or less (GLNPO unpublished data), so a reduction in phytoplankton populations would not necessarily be expected to result in a measurable increase in transparency. Suspended solids inputs to the western basin of Lake Erie are quite high; the main source of particulates, the Maumee River, delivers up to 1.3 million metric tons/year of suspended sediment to the lake (Richards 2002). It is likely that inputs of particles overwhelm *Dreissena* filtering capacity, particularly in April when peak loads occur. Sediment resuspension could also help prevent dreissenid-related de-

creases in turbidity in both the western and central basins. At a depth of 20 m, close to the maximum depth of the central basin, waves with a height of only 0.5 m can produce disturbance at the sediment surface (Charlton and Lean 1987). Resuspension events are even more likely in the shallower western basin (Lick *et al.* 1994). Additionally, differential assimilation of algal and non-algal particulates by *Dreissena* could lead to a greater permanent removal of algal, compared to non-algal, particulates from the water column, and also result in a greater proportion of the non-algal particulates, in the form of feces and/or pseudofeces, being returned to the water column. In this way, systems dominated by non-algal particulates, such as the western basin of Lake Erie, could exhibit minimal dreissenid-induced impacts on water clarity, in spite of reductions in phytoplankton populations (Roditi *et al.* 1997). This appears to have been the case in the Hudson River, NY, where *Dreissena* colonization resulted in a large (~90%) reduction in algal and microzooplanktonic biomass, but only a 7% increase in water transparency, presumably due to resuspension of feces and pseudofeces (Pace and Caraco, cited in MacIsaac 1996).

While modest decreases in summer chlorophyll *a* were seen in the central and eastern basins, these were undoubtedly due at least in part to reductions in phosphorus, rather than filtering impacts of dreissenids. Summer total phosphorus concentrations in the central and eastern basins have declined since the dreissenid invasion (Makarewicz *et al.* 2000), and for the period of our study post-dreissenid concentrations were, on average, about 20% lower than pre-dreissenid concentrations (GLNPO, unpublished data). The thermal stratification which exists in these two basins during the summer would also seem to preclude substantial direct filtering impacts of benthic mussels. In contrast, total phosphorus concentrations in the western basin decreased by only about 8% between the two periods, while chlorophyll *a* decreased by nearly 50%. Unlike the other two basins, the western basin remains largely unstratified during the summer, and thus the entire water column is theoretically accessible to filtration impacts.

The lack of a *Dreissena*-related increase in transparency in the shallower portions of Lake Erie is perhaps surprising given previous estimates of both mussel density and filtering capacity. MacIsaac *et al.* (1992) estimated that the population densities of $2.7 \times 10^5/\text{m}^2$ observed on Hen Island Reef in the western basin had the potential to filter the 7 m water column between 3.5 and 18.8 times per day. *Dreissena* distribution in the western basin is highly

patchy, however, with mussels largely absent from most soft bottomed sites. As a result, basin-wide densities are probably much lower than early estimates derived from hard substrates might suggest. As part of a lake-wide survey, Jarvis *et al.* (2000) estimated basin-wide densities to be only 418/m² in 1998. Assuming an average filtering rate of 34.9 mL/ind/hr (Jarvis *et al.* 2000), this results in an average turnover time for the entire western basin of approximately 20 days. The eastern basin, while much deeper than the other two basins, currently supports the highest *Dreissena* densities in Lake Erie, with numbers reaching 31,208/m² in the northwestern region of the basin, and an estimated basin-wide average density of 4,826/m² (Jarvis *et al.* 2000). Dermott *et al.* (1998) arrived at a substantially higher basin-wide average density (14,147/m²) on the basis of cores collected from a submersible. Using data from Jarvis *et al.* (2000), the average turnover time for the eastern basin would be approximately 7.6 days. Graham *et al.* (1996), using data from 1993, calculated a basin-wide turnover time of approximately 2.3 days. While estimates of dreissenid densities, and consequently estimates of water column turnover times, are subject to substantial variability (cf. Vanderploeg *et al.* 2002), it does appear that during the unstratified period dreissenid filtration can impact particle concentrations in the eastern basin, in spite of its greater depth, due at least in part to larger mussel populations there.

Unlike the situation in spring, when the basin was unstratified, the marked decrease in epilimnetic turbidity in the eastern basin during summer was probably not the result of direct filtration effects of dreissenids, since stable thermal stratification exists during this period. Instead, we believe that an indirect effect of the dreissenid invasion might be responsible, at least in part, for the reduction in turbidity seen during the summer. Lake Erie is supersaturated with respect to calcium during the summer, and the eastern basin, and to some extent the central basin as well, has been shown to be subject to whiting events (Strong and Eadie 1978). It is possible that calcium uptake by burgeoning dreissenid populations since the 1990s has reduced calcium levels enough to lessen the frequency and/or intensity of whiting events, thus accounting for the generally lower summer turbidity values seen since the *Dreissena* invasion. While data on open water calcium concentrations in Lake Erie are not currently available, spring alkalinity in the central and eastern basins decreased by approximately 10 mg CaCO₃/L in the 6 years following the dreissenid invasion

(GLNPO, unpublished data), which would be consistent with a decreased tendency of whiting event occurrence. Further work is needed to fully determine the plausibility of this hypothesis.

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